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PLECTROTAXY AS A SYSTEMATIC CRITERION IN LITHOBIOMORPHIC CENTIPEDES (CHILOPODA: LITHOBIOMORPHA)¹

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Since 1862, when Ludwig Koch first employed plectrotaxic ² criteria, the number and disposition of the stout articular spurs of the lithobiid centipedes have played a major role in the systematics of the group and of the order to which it belongs. In that year Koch augmented his descriptions with notes on the ventral spurs of the ultimate legs. Proceeding along the same lines, Meinert in 1872 noted the ventral spurs of the ultimate and first legs. In 1880 Latzel, responsible for so many innovations in the study of the Myriapoda, employed the dorsal and ventral plectrotaxy of the first, fourteenth, and fifteenth pairs of legs as correlative systematic criteria. C. H. Bollman in his short but prolific period of publication in the 1880's followed Meinert and Koch. No doubt influenced by Latzel and Bollman, Chamberlin and Verhoeff at about the turn of the century embarked upon a relatively new phase of lithobiid systematics with their pronounced emphasis upon the plectrotaxy of all the legs as

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² Plectrotaxic, from plectrotaxy $(\pi\lambda\epsilon\kappa\tau\rho\rho\nu=\text{calcar}=\text{spur})$, the arrangement and nomenclature of the pedal spurs of lithobiomorphous centipedes. I devised and published this term many years ago because other terms, e.g., Broelemann's "spinulation," were inappropriate in that they refer to spines. The difference between spines and spurs is important and worth stressing again. In accordance with the usage of Constock, Snodgrass, and others, a spur is a movable multicellular alveolate outgrowth of the exoskeleton. A spine by contrast is an immovable multicellular nonalveolate outgrowth of the exoskeleton.

specific and generic criteria. This tendency is particularly evident in the work of R. V. Chamberlin, whose systematic outlook has been more or less dominated by the consideration of pleetrotaxy, especially at the specific level.

The approach used by all these authors might well be termed the classical or, better, the quantitative one because it takes into account the numbers of spurs on the various leg articles, as the following example illustrates.

Let us consider the tenth leg of the cosmopolitan species *Lithobius* forficatus (Linné) (see fig. 1). It is clear that the prefemur, femur, and the tibia each bear a number of stout distal spurs. The prefemur bears three dorsal spurs, the femur and tibia each bear two. Ventrally the prefemur and femur each bear three spurs and the tibia two. The coxa, trochanter, and tarsus are spurless dorsally and ventrally.

The number and articular association of these spurs has traditionally been expressed as a fraction. The ventral spurs are then indicated in the position of the denominator, the dorsal spurs in the position of the numerator. The disposition of the spurs on each surface, dorsal and ventral, of the leg is expressed as a series of five figures, each of which refers to the number of spurs upon the indicated leg article. For example, the formula $\frac{0,0,3,2,2}{0,0,3,3,2}$ is that of the tenth leg discussed above. Reading from left to right, it is easily seen that the first two articles (coxa and trochanter) have no spurs, that the prefemur dorsally has three, the femur two, and the tibia two. The ventral plectrotaxy is similarly determined.

The fact that this quantitative representation is obviously convenient accounts for its popularity. The formulae are readily determined and recorded; they can be expressed in a minimum of space (a not unimportant advantage in these days of high printing costs); they convey considerable information graphically and quickly. Quantitative formulae, however, can tell us only how many spurs are borne upon the various leg articles; they fail to tell us which spurs are present or absent.

Qualitative Plectrotaxy

This considerable disadvantage was probably first fully appreciated by Henri Ribaut who, in 1921, published a short paper describing his own innovation, which takes into consideration not only the number of spurs present, but also the identity of those spurs as well as the identity of the spurs that are absent. Because his system stresses which particular spurs are absent and present, I have termed it qualitative plectrotaxy. In spite of its many obvious advantages the qualitative method of Ribaut was not employed by others until Broelemann published his monograph on the French chilopod fauna in 1930, at which time he incorporated the Ribaut formulae in the description of each species. Unfortunately, even this impetus, expertly and extensively utilized in a work of paramount importance, was insufficient to attract contemporary interest.

--pretarsus tarsus 2tarsus 1-DTiA-DTIP tibia--FIGURE 1 .- Tenth leg of Lithobius forficatus (Linné). Dorsal aspect, setae deleted, spurs solid in black. Leg articles, lower-case letters; leg DFP DFA spurs, upper-case letters. condyle femur DPM prefemurtrochanter

The Ribaut System and Subsequent Useful Modifications

Examining again the dorsal surface of the tenth prefemur of L. forficatus, we see that one of the three spurs is situated just cephalad of the dorsal prefemoral condyle, a second spur is located just caudad of the condyle, and the third spur arises from the extreme caudal surface of the article. This arrangement is typical of spurs on any leg article: it includes all the spurs that usually occur on one side. It is an arrangement that undergoes modification in various other species, almost always by depletion, or, in a very few forms, by the addition of supernumerary spurs on the last one or two pairs of legs. Ribaut designated the precondylic spur as the anterior spur, the postcondylic spur as the medial, and the caudal spur as the posterior. Ribaut indicated the prefemur with the upper-case letter P, the leg's dorsal surface with a lower-case d, and the anterior, medial, and posterior spurs with the lower-case letters a, m, and p, respectively. In this fashion he was able to identify every spur of the animal's leg. Thus, daP refers to the anterior dorsal spur of the prefemur; dmP refers to the medial dorsal spur of the same article.

In my publications I have employed the qualitative approach of Ribaut but have slightly modified its terminology for greater clarity and utility, and to bridge the purely linguistic discrepancy between French and the more acceptable Greco-Latin root-words that are universally understood and employed by zoologists. My revised formularization involves three upper-case letters. The first (from the left) refers to the surface of the leg (dorsal or ventral), because when one examines a specimen, dorsal or ventral orientation is the first consideration taken into account. The second letter refers to the leg article: C, coxa; Tr, trochanter; P, prefemur; F, femur; Ti, tibia. Note that a second and lower-case letter conveniently distinguishes between trochanter and tibia. The third letter refers to the particular spur: A, anterior; M, medial; P, posterior. Thus, DPA refers to the anterior spur dorsally on the prefemur. In fig. 1 the several spurs are labelled.

This system lends itself readily to a variety of useful presentational schemes. The format presented here is probably the most useful in that it conveys a maximum of information at a glance and in addition can be readily adapted to derivative schemes of a more specialized nature. The format illustrated in this paper is a slight modification of that published by Broelemann in 1930. The reader is referred to table 1.

The numbers in the first column refer to the 15 pairs of legs. Columns are provided for the descriptive codes representing the coxa, trochanter, prefemur, femur, and tibia under the headings "Dorsal" and "Ventral." Thus, each intersection of a vertical column with a horizontal column represents a particular leg article of a particular leg, and the letters in each such intersection show which spurs thereupon are present and absent. For example (see table 1 for *Lithobius forficatus*), beneath "Dorsal" and "P" and opposite 10 we find the letters AMP. Beneath "Ventral" and "Tr" and opposite 15 we find only the letter M. Finally, note that an italic letter means that that spur is variable in that position, that is, it may be either present or absent.

Quantitative formulae are readily derived from such a format. Merely by adding the letters in each square for a given leg we may calculate that leg's quantitative plectrotaxic formula. Thus for L. forficatus, tenth leg, dorsal, by adding letters we derive the quantitative formula 0,0,3,2,2.

Owing to the peculiar modification of the ultimate coxa, its plectrotaxy requires further clarification. Ribaut interpreted its dorsal spur as being homologous with an anterior spur of a more anterior leg; consequently, Ribaut and Broelemann both refer to it as vaH=VCA. Although their homologization is undoubtedly accurate, for purely practical reasons it seems preferable to treat the lateral armature (VCA) separately and not in the same chart with the others. Chamberlin and others, including myself, have followed this practice, referring to these special spurs merely as "lateral spurs" or "lateral armature".

Discussion and Some Applications

The great value of Ribaut's qualitative method is that it facilitates analysis as well as pure description; it does so because it takes cognizance of the fact that the spur series of the homologous legs are themselves serially homologous. Studying the plectrotaxy chart for L. forficatus, we see that DPA occurs on every leg and that all the DP spurs are serially homologous because all occupy homologous positions on successive legs. Considering the femoral spurs, we note that DFA occurs on legs 1 through 10 or 11, but that it is absent on legs 12 through 15; this variation helps to illustrate a second important point. A careful study of many lithobiid forms shows that once any given spur makes its initial appearance upon an anterior leg, its serial homologues will be present without interruption (except in monstrosities) upon all succeeding legs until the posterior limit of the series is reached. Thus, in Nadabius pullus (Bollman), DTiP makes its first appearance on leg 3 and reaches its posterior-most limit on leg 14 without interruption (see table 2). VPA does not appear anterior to leg 11, after which it continues uninterrupted to leg 15.

One of my additions to the Ribaut system has been to formularize such information, that is, to indicate by a convenient formula those legs upon which any given spur series occurs. It is possible to formularize such a dispersion, as Ribaut has termed it, only because of the serially homologous nature of the spurs. In *L. forficatus*, DPM occurs on legs 1–15 and is easily and clearly represented by the formula DPM=1–15. Similarly, DFA occurs on legs 1–10 or 1–11 and is formularized by DFA=1–10, 11. To refer to any single spur without regard to its dispersion, we simply write, for example, DTiP(7) (DTiP of the seventh leg).

A slight modification of this form of representation is useful for indicating the quantitative plectrotaxy of a given leg and surface thereof. Thus the formula D15=10310 means that the ultimate leg's dorsal quantitative formula is 1,0,3,1,0. A typical ventral formula might be V15=01332.

Relative to plectrotaxy in general as it pertains to systematics, a few conclusions will be drawn and some contingent factors noted. Again, of fundamental importance is our recognition of the serially homologous nature of the spurs: it is this feature which discloses the inherent order and system in plectrotaxy and, for the practical purposes of systematics, facilitates prediction and analysis.

Because these spurs occur in a serially unbroken sequence in normal mature specimens,³ Ribaut was impressed with the possible importance of the anterior and posterior limits of the various spur series. He suggested that these series are subject to variations, e.g., of age, of ontogenetic factors, of systematic position. His studies showed him that the anterior limits of dispersion are quite variable intraspecifically, but that the posterior limits of different spur series tend to be more constant interspecifically. Ultimately he hesitated to use anterior dispersional limits as diagnostic criteria and instead stressed the use of posterior limits: ". . . en considérant les limites de la zone de dispersion de chaque aiguillon, on s'apercoit que la postérieure est bien plus caractéristique de l'espèce que l'antérieure, moisis soumise aux variations individuelles et plus indépendante de l'âge des individus. J'ai remarqué, en outre, que la spinulation du fémur et du tibia, à l'exception de vmF VFM, que existe toujours en 15, est bien plus variée, suivant l'espèce, dans ses limites postérieures que celle du préfémur, du trochanter et de la hance."

His reference to the age of the individual is a factor of extreme importance, for, as a general rule, the older the specimen, the farther forward most of the spur series extend. For this reason, it is most important to take into consideration the age of the specimen when interpreting plectrotaxy in order to avoid confusing, let us say, a praematurus form of one species with a maturus specimen of another closely related species. I have no doubt that many "species" owe their existence to this very error. As we shall see, an immature *Nadabius aristeus* Chamberlin could be confused with a mature *N. pullus* (Bollman), if other nonplectrotaxic criteria were discounted. In this connection, it is important to point out that there are many lithobiid species, so called, distinguishable from other species solely on the basis of plectrotaxy.

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³ It is important to note that in immature forms, series VPA, VFA, and VFM are frequently discontinuous. That is, an anterior spur may be present, let us say, ou the third femur ventrally, but may be wanting upon the succeeding two or three legs only to reappear on a more posterior leg. I have observed this phenomenon much more frequently in specimens in the anamophic phase of development than in specimens in the later epimorphic developmental phase. Apparently the chance that a given spur series will be discontinuous is far greater before the adult complement of legs has been acquired. Thereafter discontinuity does occur in immature forms, but is apparently extremely rare.

Ribaut suggested that anterior-spur dispersions are generally not to be trusted in separating species, a point of view which perhaps implies a static notion of what a species is and a rather broad interpretation of specific limits. Wide discrepancies in anterior dispersion often do parallel other nonplectrotaxic characters which may be invoked to distinguish species; however, I find that the much more constant posterior limits of dispersion are often characteristic of what are either species groups, or, as Chamberlin thought, genera and subgenera. I do not mean to suggest that this correlation invariably exists, only that the relationship may very well be widespread. A good example is seen in the genus *Nadabius*.

Three species that may be separated on satisfactory nonplectrotaxic criteria and that also reflect their specific individualities by plectrotaxy are *Nadabius pullus* (Bollman), *aristeus* Chamberlin, and *iowensis* (Meinert). Fortunately, they are relatively common, and at least two, *pullus* and *aristeus*, are now known to be fairly widespread, at least in the eastern United States. A large number of specimens of each species was examined, and the plectrotaxy of each specimen was recorded. This information is summarized in tables 8 and 9.

Let us consider anterior dispersion first, as shown in table 8. In the vertical column at the left, the spur series are listed in order. In the three double columns to the right, anterior dispersions for the three species are summarized. Within each double column the figures to the left show the number of the anterior-most leg upon which that particular spur was observed, and the figures to the right in each double column show the number of the posterior-most leg upon which the same spur series was observed to commence. For example, in the *pullus* species, the spur series DPA spur reaches its anterior dispersional limit on legs 9 through 12.

Table 9 similarly depicts posterior limits of dispersion. With the exception of two spur series, all the posterior dispersions for the three species are seen to be identical. Of the two interspecifically varying dispersions of spur series, DFA and DTiA, that by the latter is more reliable, and, when coupled with other characters could be used to distinguish iowensis from pullus and aristeus. Inasmuch as the significant similarity of all the posterior dispersions in these forms parallels other morphological nonplectrotaxic criteria, the three forms constitute a phylogenetic end-product of unquestionable homogeneity. They comprise an assemblage which would be called a species group, a subgenus, or a genus, depending upon one's point of view. Therefore, posterior dispersion appears to be more indicative of categories above the species level than solely of species, as Ribaut contended. This concept of course is relative and provisional and depends upon how one interprets the three forms as a group. I am fairly certain that the three are closely related but discrete species.

As we shall see now, anterior dispersions will separate the three forms considered here, but great care must be exercised in distinguishing significant from nonsignificant series. DCA and VPA, for example, cannot be relied upon as interspecific criteria, though aristeus and iowensis may easily be distinguished from pullus on the basis of the anterior dispersion of VPM. In the first two species, VPM begins regularly (in mature forms) on legs 1 or 2, whereas in *pullus* it makes its initial appearance on legs 7, 8, 9, or 10. VFP similarly shows significant interspecific and nonoverlapping variability of dispersion. Dispersion of DPA is also satisfactory although a less reliable criterion than that of VFP. Because there is no overlap between VPM and VFP, dispersion of these series might be safely used as diagnostic key characters, even in identifying single specimens. Perhaps if the plectrotaxy of an enormous series of specimens were analyzed, dispersion of other spur series would also prove to be indicative of interspecific identity.

To a large extent the classical quantitative consideration of spurs overlooks dispersional variability, or else it does not (because it cannot) treat it effectively. For this reason, many forms that are today viewed as discrete species purely on the basis of plectrotaxy will eventually be recognized as intraspecific variants.

My studies have revealed another important factor which I believe holds true throughout the order. The more posterior legs acquire their adult spur complement first and thereafter the spur series extend progressively cephalad during anamorphic and most of epimorphic growth, that is, the last legs to acquire the adult complement of spurs are the most anterior ones. This phenomenon alone necessitates the examination of an adequate number of fully mature specimens if interspecific characters are sought in anterior dispersional limits.

Ribaut cited the following as the spur series most significant in relation to intraspecific constancy in posterior dispersions: FVA, VFP, VTiA, VTiM, DFA, DFP, DTiA, and TDiP. I believe this thesis is very often true in respect to groups of closely related species, but, as explained above, posterior dispersional limits are often similar or identical in closely related but distinct species.

I have found plectrotaxy of greatest utility in those instances where an entire spur series is lacking, or where all or a part of a rare spur series is present. Illustrative of the first condition (see table 7) is *Taiyubius harrielae* (Chamberlin), whose only ventral tibial spur is VTiM; the vast majority of lithobiids of this general habitus have in addition VTiA. Similarly, the presence of VTiP in some of the *Neolithobius* species, though not unique by any means, is at the same time distinctive and almost always useful as a diagnostic device. The striking scarcity of entire spur series in Monotarsobius, Nampabius, and Sigibius, upon analysis, is of considerable diagnostic utility. Thus, in Nampabius fungiferopes Chamberlin (table 5), only four series are regularly present: DTiA, VTrM, VPM, VTiM. A fifth series, VFM, may or may not manifest itself by a single spur on leg 13. A related form, Nampabius virginiensis Chamberlin (table 6), characteristically and in contrast lacks only DCA, DPA, VCM, VPA, VFP, VTiA, and VTiP; it thus exhibits series never observed in fungiferopes but at the same time lacks series commonly seen in the majority of North American Lithobiinae. This criterion, the complete and consistent absence of an entire spur series, is surely the most reliable of plectrotaxic characters. It is either of specific or of higher categorical significance.

Finally, it is obviously of prime importance to determine how dispersion may be correlated with age. In investigating the ageplectrotaxy factor, *N. pullus* and *aristeus* were selected. The plectrotaxy of a typical praematurus and of a typical maturus is summarized in tables 10 and 11. The double column on the left shows the anterior dispersional limits of the various series for a praematurus and for a maturus specimen. The right-hand column presents posterior dispersional data for the same two age variants.

It is apparent that posterior dispersion in *pullus* is inconclusive but that certain spur series clearly reflect anterior variation as a function of age; VPP varies considerably and is perhaps the best indicator, but the age factor is also manifest in VTiA, DPM, and VFP, all on the anterior limits side of the chart. The remaining series appear to be unreliable.

A somewhat similar picture is seen in *aristeus* (table 11). Here VFP, VTiA, and VPP are excellent indicators of immaturity, but DPM does not appear to be meaningful. Such data cannot fail to impress one with the dangerous possibilities inherent in designating a new form solely on the basis of a single specimen's ventral quantitative plectrotaxy without regard to valid non-plectrotaxic correlative criteria. Nonetheless, this very practice has plagued lithobiid systematics in the United States and abroad in the past, and it still enjoys great favor today.

			Dorsal					Vent	ral	
Leg pair	\overline{C}	Tr	P	F	Ti	\overline{C}	Tr	P	F	Ti
1	~		AMP	AP	AP	-		MP	AMP	AM
2			AMP	AP	AP			MP	AMP	AM
3		_	AMP	AP	AP			MP	AMP	AM
4			AMP	AP	AP	-	\mapsto	AMP	AMP	AM
5	-		AMP	AP	AP	-	-	AMP	AMP	AM
6			AMP	AP	AP	B 1	***	AMP	AMP	AM
7	-		AMP	AP	AP	· · · · ·	~~~~	AMP	AMP	AM
8	-		AMP	AP	AP			AMP	AMP	AM
9		_	AMP	AP	AP			AMP	AMP	AM
10	~~	_	AMP	AP	AP			AMP	AMP	AM
11			AMP	AP	AP		-	AMP	AMP	AM
12	Α		AMP	P	AP	-		AMP	AMP	AM
13	A		AMP	Р	P		Μ	AMP	AMP	AM
14	A		AMP	Р	Р		Μ	AMP	AMP	AM
15	Α	-	AMP	\mathbf{P}	-	-	М	AMP	AMP	$\mathbf{A}\mathbf{M}$

TABLE 1.—Qualitative plectrotaxy of Lithobius forficatus (Linné)

TABLE 2.—Qualitative plectrotaxy of Nadabius pullus (Bollman)

			Dorsal					Ventr	al	
Leg pair	\overline{C}	Tr	P	F	Ti	\overline{C}	Tr	\overline{P}	F	Ti
1		-	MP	Α	Α	-	-	P	AM	Μ
2		_	MP	AP	A	-		Р	AM	AM
3	_		MP	AP	AP			Р	AM	AM
4	-		MP	AP	AP		_	Р	AM	AM
5		_	MP	AP	AP		_	Р	AM	AM
6			MP	AP	AP	-		Р	AM	AM
7			MP	AP	AP	-		MP	AM	AM
8	-		AMP	AP	AP	-	-	MP	AM	AM
9		_	AMP	AP	AP			MP	AMP	AM
10	_		AMP	AP	AP			MP	AMP	AM
11		-	AMP	AP	AP	-		MP	AMP	AM
12	A		AMP	AP	AP	-		AMP	AMP	AM
13	A		AMP	AP	AP		M	AMP	AMP	AM
14	\mathcal{A}		AMP	Р	\mathbf{P}		Μ	AMP	AMP	AM
15	А	-	AMP	Р	-	-	М	AMP	AMP	A

TABLE 3.—Qualitative plectrotaxy of Nadabius aristeus Chamberlin

			Dorsal					Vent	ra l	
Leg pair	\overline{C}	Tr	P	F	Ti	C	Tr	P	F	Ti
1			MP	AP	Α			MP	AMP	AM
2	-	-	MP	AP	Α			MP	AMP	AM
3			MP	AP	AP		_	MP	AMP	AM
4	_		AMP	AP	AP		-	MP	AMP	AM
5	-		AMP	AP	AP	*	⊷	MP	AMP	AM
6		-	AMP	AP	AP			MP	AMP	AM
7			AMP	AP	AP	-	-	MP	AMP	AM
8		_	AMP	AP	AP	-		MP	AMP	AM
9		-	AMP	AP	AP	-	-	MP	AMP	AM
10	_		AMP	AP	AP			MP	AMP	AM
11	-		AMP	AP	AP	-		AMP	AMP	AM
12			AMP	AP	AP			AMP	AMP	AM
13	-A		AMP	AP	AP		Μ	AMP	AMP	AM
14	Α		AMP	P	\mathbf{P}	b 1	Μ	AMP	AMP	AM
15	Α		AMP	Р	-		М	AMP	AMP	A

				Dorsal					Vent	ral	
$Leg \ pa$	ir	\overline{C}	Tr	P	F	Ti	\overline{C}	Tr	P	F	Ti
1		-	_	MΡ	AP	Α	_	_	MP	AMP	AM
2		_	_	MP	AP	AP	—	-	MP	AMP	AM
3		_	_	$A \mathrm{MP}$	AP	AP	_	_	MP	AMP	AM
4		_	_	AMP	AP	AP		_	MP	AMP	$\mathbf{A}\mathbf{M}$
$\overline{5}$		_	_	AMP	AP	AP		_	MP	AMP	AM
õ		_	-	AMP	AP	AP	_	-	MP	AMP	AM
7		_	-	AMP	AP	AP			MP	AMP	AM
8		_	-	AMP	AP	AP	-		MP	AMP	AM
<u>9</u>			_	AMP	AP	AP	_	_	AMP	AMP	AM
10		-	_	AMP	AP	AP	_	_	AMP	AMP	AM
11		A	_	AMP	AP	AP	-		AMP	AMP	AM
$\overline{12}$		\overline{A}	_	AMP	AP	AP	_	_	AMP	AMP	AM
13		A	_	AMP	Р	P	_	Μ	AMP	AMP	AM
14		Ā	_	AMP	P	P	_	М	AMP	AMP	AM
15		Ā	_	AMP	P		_	М	AMP	AMP	A

TABLE 4.—Qualitative plectrotaxy of Nadabius iowensis (Meinert)

TABLE 5.—Qualitative plectrotaxy of Nampabius fungiferopes (Chamberlin)

			Dorsal					Vent	ral	
Leg pair	\overline{C}	Tr	P	F	Ti	\overline{C}	Tr	P	F	Ti
1	_	_	-	_	A	-	_	_	-	-
2	—	_	_	-	A	_	_	-	-	-
3	_	_		-	Α	-	_	-		—
4	_	-	_	-	A	_	-	-	_	M
$\frac{4}{5}$			_		A	-	_	-	—	M
6	_		_	_	Α	_	-		_	M
7	_	_		-	Α	_	_	-	-	\mathbf{M}
8	_	_		_	Α	_	_	-		\mathbf{M}
9	_	_	_	-	Α	-	_	-	_	\mathbf{M}
10	-	_	_		Α		_	-	-	\mathbf{M}
11	_		_	_	A	—			-	\mathbf{M}
12	_	-	-		A	_	_			M
13		_			-		_	-	M	M
14	_	_	_			_	M	Μ	M	~
15	-	_			_	****	M	Μ	-	-

TABLE 6.—Qualitative plectrotaxy of Nampabius virginiensis Chamberlin

			Dorsa	l				V	entral	
Leg pair	\overline{C}	Tr	P	F	Ti	\overline{C}	Tr	\overline{P}	F	Ti
1				A	A	_			-	
2	-	_		A	Α	_		~~*	-	
3		_	***	-A	Α				-	M
4	_	_		A	AP					\mathbf{M}
5	-	~~*	~~*	A	AP				M	\mathbf{M}
6		_		Α	AP				М	\mathbf{M}
7	_	~~	_	A	AP				AM	\mathbf{M}
8			-	AP	AP		_		AM	M
9				AP	AP	-	_		AM	\mathbf{M}
10	_	-	_	AP	AP		~~		AM	\mathbf{M}
11		_		AP	AP		~~*	-	AM	\mathbf{M}
12		_	MP	AP	AP	-	-	M	AM	\mathbf{M}
13		_	MP	AP	-		-	MP	AM	M
14		_	MP	-		_	Μ	MP	Μ	
15		_	MP	~~*			Μ	MP	M	-

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TABLE 7.—Qualitative plectrotaxy of Taiyubius harrielae (Chamberlin)

			Dorsal					Vent	ral	
Leg pair	\overline{C}	Tr	P	F	Ti	\overline{C}	Tr	P	F	Ti
1	-		MP	AP	Α		-	MP	AMP	Μ
2			AMP	AP	A		_	MP	AMP	Μ
3			AMP	AP	AP		-	MP	AMP	\mathbf{M}
4	-	_	AMP	AP	AP			MP	AMP	M
5			AMP	AP	AP	—		MP	AMP	Μ
6			AMP	AP	AP	-	-	MP	AMP	\mathbf{M}
7		-	AMP	AP	AP			MP	AMP	Μ
8	-	-	AMP	AP	AP			MP	AMP	\mathbf{M}
9	-	-	AMP	AP	AP			MP	AMP	\mathbf{M}
10	-	_	AMP	AP	AP			MP	AMP	\mathbf{M}
11		-	AMP	AP	AP			AMP	AMP	Μ
12	A	_	AMP	AP	AP		M	AMP	AMP	\mathbf{M}
13	Α	_	AMP	Р	P		\mathbf{M}	AMP	AMP	\mathbf{M}
14	Α	_	AMP	Р	Р		\mathbf{M}	AMP	AMP	Μ
15	A		AMP	Р	-		\mathbf{M}	AMP	AMP	~

TABLE 8.—Anterior limits of spurs on Nadabius

	Spur series	pul	lus	arist	eus	iowe	nsis
DCA		13	14	12	13	11	13
DPA		9	12	4	8	3	7
DPM		1	2	1	1	1	1
DPP		1	1	1	2	1	1
DFA		1	1	1	1	1	1
DFP		2	2	1	2	1	1
DTi	ł	1	1	1	1	1	1
DTil	2	3	4	3	4	2	3
VTrl	M	13	14	13	13	13	13
VPA		12	13	11	12	9	12
VPM	[7	10	1	2	1	2
VPP		1	2	1	2	1	1
VFA		1	2	1	1	1	1
VFM	[1	2	1	1	1	1
VFP		9	12	1	3	1	1
VTi/	1	2	6	1	3	1	2
VTiN	1	1	1	1	1	1	1

TABLE 9.—Posterior limits of spurs on Nadabius

Spur series	pullus	aristeus	iowensis
DCA	15 15	15 15	15 15
DPA	15 15 15	15 15 15	15 15
DPM	15 15	15 15	15 15
DPP	15 15	15 15	15 15
DFA	12 13	13 13	11 12
\mathbf{DFP}	15 15	$15 \ 15$	15 15
DTiA	13 13	13 13	12 12
DTiP	$14 \ 14$	14 14	$14 \ 14$
VTrM	15 15	15 15	15 15
VPA	15 15	15 15	15 15
VPM	$15 \ 15$	15 15	15 15
VPP	$15 \ 15$	$15 \ 15$	15 15
VFA	15 15	$15 \ 15$	15 15
\mathbf{VFM}	$15 \ 15$	$15 \ 15$	15 15
VFP	$14 \ 15$	$15 \ 15$	15 15
VTiA	14 15	15 15	15 15
VTiM	14 14	$14 \ 14$	$14 \ 14$

	Anterio	or limits	Posterior limits			
Spur series	Praema- turus	Maturus	Praema- turus	Maturus		
DCA	14	14	15	15		
DPA	13	10	15	15		
DPM	11	2	15	15		
DPP	1	1	15	15		
DFA	1	1	13	13		
DFP	2	2	15	15		
DTiA	1	1	13	13		
DTiP	4	3	14	14		
VTrM	13	13	15	15		
VPA	13	12	15	15		
VPM	11	8	15	15		
VPP	11	1	15	15		
VFA	6	1	15	15		
VFM	3	1	15	15		
VFP	13	10	15	15		
VTiA	10	4	14	14		
VTiM	1	1	14	14		

 TABLE 10.—Age correlation of Nadabius pullus (Bollman)

TABLE 11.—Age correlation of Nadabius aristeus Chamberlin

	Anter	ior limits	Posterior limits				
- Spur series	Praema- turus	Maturus	Praema- turus	Maturus			
DCA	14	12	15	15			
DPA	10	6	15	15			
DPM	2	1	15	15			
DPP	1	1	15	15			
DFA	1	1	12	13			
DFP	2	3	15	15			
DTiA	1	1	12	13			
DTiP	5	3	14	14			
VTrM	13	13	15	15			
VPA	13	12	15	15			
VPM	3	1	15	15			
VPP	11	1	15	15			
VFA	2	1	15	15			
VFM	1	1	15	15			
VFP	12	1	15	15			
VTiA	7	1	14	15			
VTiM	1	1	14	14			

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